

## ESTIMATION OF SEX-SPECIFIC SURVIVAL FROM CAPTURE–RECAPTURE DATA WHEN SEX IS NOT ALWAYS KNOWN

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**Abstract.** Many animals lack obvious sexual dimorphism, making assignment of sex difficult even for observed or captured animals. For many such species it is possible to assign sex with certainty only at some occasions; for example, when they exhibit certain types of behavior. A common approach to handling this situation in capture–recapture studies has been to group capture histories into those of animals eventually identified as male and female and those for which sex was never known. Because group membership is dependent on the number of occasions at which an animal was caught or observed (known sex animals, on average, will have been observed at more occasions than unknown-sex animals), survival estimates for known-sex animals will be positively biased, and those for unknown animals will be negatively biased. In this paper, we develop capture–recapture models that incorporate sex ratio and sex assignment parameters that permit unbiased estimation in the face of this sampling problem. We demonstrate the magnitude of bias in the traditional capture–recapture approach to this sampling problem, and we explore properties of estimators from other ad hoc approaches. The model is then applied to capture–recapture data for adult Roseate Terns (*Sterna dougallii*) at Falkner Island, Connecticut, 1993–2002. Sex ratio among adults in this population favors females, and we tested the hypothesis that this population showed sex-specific differences in adult survival. Evidence was provided for higher survival of adult females than males, as predicted. We recommend use of this modeling approach for future capture–recapture studies in which sex cannot always be assigned to captured or observed animals. We also place this problem in the more general context of uncertainty in state classification in multistate capture–recapture models.

**Key words:** capture–recapture models; classification by sex; Roseate Terns; sex-specific survival rates; *Sterna dougallii*; uncertain state assignment.

### INTRODUCTION

Demographic parameters and sampling probabilities frequently vary as a function of various state variables characterizing animals. For example, age, sex, reproductive condition, and body mass are all potential influences on such quantities as survival and capture probability. Some state variables such as sex are constants (in most vertebrate species) that do not change over the life span of the individual. In capture–recapture analyses, such variables are typically dealt with as group effects, with general models permitting all survival and capture probabilities to differ among groups and reduced-parameter models imposing various equality constraints among parameters of the different groups (e.g., Lebreton et al. 1992, Williams et al. 2002). Other state variables, such as age, exhibit deterministic variation over an animal's life span, and capture–recapture models implementing such deterministic transitions have been developed (Pollock 1981, Lebreton et al. 1992, Williams et al. 2002). Finally, some state

variables such as body mass and reproductive condition exhibit stochastic variation over an animal's life span, and multistate capture–recapture models permit estimation in the face of such stochastic, state-specific variation (Arnason 1972, Nichols et al. 1992, 1994, Fujiwara and Caswell 2002, Williams et al. 2002).

Most previous capture–recapture modeling work has assumed unambiguous assignment of captured or observed animals to state. That is, a captured or observed animal can be assigned to the proper sex, age, mass, or reproductive condition category with certainty. Recent acknowledgment of uncertainty in state assignment has led to modeling approaches for dealing with such uncertainty. Fujiwara and Caswell (2002) and Lebreton and Pradel (2002) considered very general approaches in which “stage-assignment” matrices are incorporated into multistate capture–recapture models. These matrices contain probabilities associated with an animal being in each possible state at each capture/observation occasion. These probabilities can be assumed to be known and are typically obtained from ancillary data (see Fujiwara and Caswell 2002). If these assignment probabilities are not assumed to be known, then identifiability problems may arise. This approach is general and can be used with all of the classes of state variables described above.

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Kendall et al. (2003) considered uncertainty in state assignment for multistate models with stochastic state transitions. Instead of using a matrix of known assignment probabilities, they used a robust capture–recapture design (Pollock 1982, Kendall et al. 1995) in which sampling is conducted at two temporal scales. Capture–recapture data over secondary periods occurring within a particular season (i.e., within a primary period [Pollock 1982]) are used to estimate a classification probability parameter, and this parameter is incorporated directly into the multistate capture–recapture modeling. The specific application involved the reproductive state of adult female Florida manatees (*Trichechus manatus latirostris*), and the uncertainty involved whether adult females were with calf or not (Kendall et al. 2003). Repeat observations of individuals with calves in a season provided the information needed to estimate a probability of correct classification,  $P(\text{detection of calf} \mid \text{female with calf})$ , and this probability was incorporated into the multistate models directly. An advantage of this approach is that it explicitly incorporates uncertainty in estimation of the classification probabilities, rather than treating these probabilities as known constants. The application and associated modeling were specific to the manatee problem, but the basic approach should be much more general and applicable to any sampling situation in which secondary samples provide the extra information needed to estimate correct assignment probabilities.

The use of the robust design in the case of state uncertainty for multistate models with stochastic transitions is necessitated by the need to have a period over which animal state cannot change, during which correct assignment probability can be estimated. Multiple observations of animals known to be in a particular state are needed in order to estimate the probability of correct assignment. However, in models with state variables that do not change over time (e.g., sex), or change in a deterministic manner (age), it should be possible to estimate correct assignment probabilities even with data collected under a standard, open-model design with a single sampling occasion per season or year. Thus, if we are ever able to assign state with certainty to some animals, then we can estimate correct assignment probabilities based on assignment information from previous and subsequent sampling periods. More importantly, we can then estimate other parameters of interest (state-specific survival and capture probabilities) in a manner that properly incorporates this classification uncertainty. Here, we apply this general approach to the problem of uncertainty about an animal's sex.

#### UNCERTAINTY IN SEX ASSIGNMENT: BACKGROUND

In many species of vertebrates, sex can be correctly ascertained for animals of virtually all ages at each sampling occasion (Dimmick and Pelton 1994). This holds true for most small mammals of trappable age

and for fledged waterfowl of most species, for example. In other situations, sex cannot be ascertained for young animals (e.g., prebreeding anurans, hatchling waterfowl) but can be determined with certainty for animals recaptured at older ages (breeding anurans, fledged waterfowl). In still other cases (e.g., many seabirds), sex cannot be easily ascertained at any age, and only display of certain behaviors (e.g., mate feeding, position during copulation) or sampling for molecular-genetic analysis permits unambiguous assignment of sex for adults. In studies of such species, it is common for sex to be unknown for the duration of the study for many individuals.

In capture–recapture studies of animals in which sex is eventually determined for a subset of animals, various data-analytic methods have been used. A common approach is to group all capture histories into three groups, animals determined at some time to have been (1) males or (2) females, and (3) animals for which sex is not ascertained during the study. Each data set is then treated as a separate group for capture–recapture modeling. For example, let “0” indicate that an animal was not caught or observed in a sample period, and let “U”, “M”, and “F” denote that an animal was caught and assigned to a category of unknown sex, male or female, respectively. Capture history 0U0F0F indicates an animal that was first caught at sample period 2 but was classified as unknown sex at that time. The animal was not caught at periods 3 or 5, but was caught and determined to be a female at period 4 and caught again at period 6. Under the typical approach to data analysis in such cases, the history would be rewritten as 0F0F0F. The only unknown sex animals would be those for which sex was never determined (e.g., 0U0U00). This naive approach is unsatisfactory, because the probability of assigning an animal to a particular group is a function of survival and capture probabilities and the realized capture history that they produce. The longer an animal lives and the more times it is seen after first release, whether due to pure chance or higher individual survival and/or capture probabilities, the more likely that it will eventually have its sex identified. In contrast, the unknown sex group will typically consist of many animals seen only once or twice and will thus produce lower survival estimates than known males or females. The male and female groups will tend to exhibit higher survival rate estimates than they should, simply because those individuals surviving to be observed in several sampling occasions have a greater probability of eventual sex assignment. This approach can thus produce biased estimates of survival and related parameters. Note that these biases do not depend on heterogeneous survival rates between or within sexes and will occur even in the case of homogeneous survival.

In addition to this inappropriate naive approach, we know of three approaches that are more reasonable, yet still not ideal. One such approach involves use of an-

cillary information in a manner similar to that of the uncertainty matrix of Fujiwara and Caswell (2002). For example, Blums et al. (1996) conducted age-specific capture–recapture analyses on waterfowl species banded as day-old ducklings, first-year birds, and adults (>1 yr old). Most ducklings were not sexed, so unsexed birds were assumed to have been 50% male based on a sample of about 6500 ducklings for which sex was determined by Blums and Mednis (1996). Of course, some ducklings were recaptured when older and their sex determined. If  $n_i$  is the number of unknown-sex ducklings released in year  $i$ , and if  $r_i^f$  denotes the number of these recaptured at least once and determined to be females, then the number of females released and never recaptured is computed as  $[(n_i/2) - r_i^f]$ . When preparing capture histories for use in capture–recapture models (e.g., Lebreton et al. 1992, White and Burnham 1999, Williams et al. 2002), this approach is thus used to determine the number of sex-specific histories with only a single “1” (single capture); e.g., 1000, 0100, 0010. If the assumed sex ratio is exactly correct, then this approach should work well. However, the approach does not incorporate uncertainty associated with the estimation of the “known” sex ratio (so variances will tend to be underestimated), and if this estimate is not close to the true sex ratio, then biased capture–recapture estimates can result.

A second approach involves use of multistate models and is most useful when sex cannot be ascertained for young animals, but is readily determined when animals attain a certain age or size. For example, Wood et al. (1998) conducted a capture–recapture study on several local populations of pig frogs (*Rana gryllio*) in northern Florida. Sex cannot be easily determined for young animals, but once animals attain adult size (80 mm snout–vent length), the diameter of the tympanum relative to that of the eye is a good indicator of sex (in adult males the tympanum is at least twice the diameter of the eye, whereas in adult females the tympanum diameter is smaller than that of the eye). Wood et al. (1998) thus used a multistate model with three classes, young (unknown sex), adult males and adult females. This approach yielded reasonable results, although survival estimates for young animals may have exhibited some bias because of heterogeneous survival in this mixed group of males and females.

A third, ad hoc approach is to simply discard all capture history data occurring prior to the time at which sex is unambiguously ascertained. For example, instead of multistate modeling with an unknown state, this ad hoc approach simply rewrites capture history 0U0F0F as 000F0F and models only that portion of the capture history occurring after the initial period at which sex is ascertained. This approach yields unbiased estimates of sex-specific survival rate and is very reasonable. Indeed, even in the multistate approach and the new approach described in this paper, we suspect that the majority of the information about sex-specific survival

comes from capture history data following identification of sex. Nevertheless, we expect the discarding of some data to carry some cost in the precision of resulting estimates.

#### SAMPLE DESIGN AND DATA

The sampling situation we envisage involves standard capture–recapture sampling for an open animal population. We thus have single-sample occasions (no robust design) followed by periods over which the population can experience gains and losses. Upon capture, we have some probability  $> 0$  that we can assess the sex of the animal with certainty. Specifically, we observe unambiguous evidence of the sex of captured males with probability  $\delta_i^M$  and of the sex of captured females with probability  $\delta_i^F$ . These probabilities correspond to the chance that an animal will exhibit unambiguous evidence, and sex of classified animals is thus considered as known. The complements of these probabilities represent the probabilities that we are uncertain about the sex of the captured animal, and thus declare the animal to be of unknown sex. Unambiguous determination of sex may involve observations of behavior (see Roseate Tern example) or morphology, and may even involve blood or tissue sampling for DNA analysis. Unambiguous determination of sex does not involve any accumulation of cues or evidence, but instead is based on evidence obtained at a single capture. The key elements of the sampling are that sex cannot be unambiguously determined for every captured animal ( $\delta_i^s < 1$ ,  $s \in [M, F]$ ), and that we only assign a sex to an animal when we are certain. Thus, designation as male and female is always correct (no misclassification error), and any uncertainty is acknowledged by designating the animal as U (unknown).

This sampling results in capture histories falling into three groups: animals identified as males at some time during the study, animals identified as females, and animals whose sex was never determined. Given this categorization, we can have two different scenarios with respect to assignment of sex in the field. One sampling situation (denoted as A) involves independent attempts to assign sex at each capture, regardless of whether sex has been assigned in a previous sampling occasion (e.g., year). In the other sampling situation (denoted as B), no attempt is made to determine sex of an animal following the initial designation of the animal as male or female. For example, consider the following capture history resulting from sampling situation A: U0F0U0. The animal was first caught in year 1 of the study, and sex could not be determined. It was next caught in year 3 and determined to be a female. In year 5, it was again caught and its sex could not be assigned based on information obtained at that capture. Under sampling situation B, this history would be written as: U0F0F0. The sex is automatically assigned at every capture following the first capture at which sex is determined, as it is with the multistate approach de-

scribed above. Of the two approaches, sampling situation B is the approach commonly used at present, but sampling situation A provides more information that can be used to estimate  $\delta_i^s$ . Even when investigators recognize the advantages associated with A, sampling situation B can still arise when investigators remember individual animals from previous years (hence cannot use subsequent observations as independent classification trials), when sex assignment is expensive of time or effort (hence not repeated following initial assignment), or when historical data bases only include the initial date at which sex is identified for each individual (so results of subsequent classification trials are not available for analysis).

#### PROPOSED MODELS

We propose a modeling approach that can be viewed as an extension of standard Cormack-Jolly-Seber (CJS) capture-recapture modeling for open populations (Cormack 1964, Jolly 1965, Seber 1965) with multiple groups (Lebreton et al. 1992). As noted above, capture histories are separated into three groups, known males, known females, and unknown sex (animals whose sex was never determined). Model parameters are defined as follows:

- $\phi_i^s$  = probability of apparent survival (survival and no permanent emigration) from period  $i$  to  $i + 1$  for animals of sex  $s$ , where  $s \in \{M, F\}$ ,
- $p_i^s$  = probability of capture in period  $i$  for animals of sex  $s$ , where  $s \in \{M, F\}$ ,
- $\chi_i^s$  = probability an animal of sex  $s$ , where  $s \in \{M, F\}$ , is never detected again after period  $i$ ,
- $\delta_i^s$  = probability that sex is ascertained in period  $i$  for an animal of sex  $s$  that is captured in period  $i$ , where  $s \in \{M, F\}$ ,
- $\pi_i^s$  = probability that an animal first released in period  $i$  is a male.

The first three sets of parameters defined above are common to CJS modeling, and  $\chi_i^s$  is not a new parameter but can be written as a function of sex-specific survival and capture probabilities (e.g., see Jolly 1965, Williams et al. 2002). The parameters new to this model are the conditional (on capture) sex assignment parameters,  $\delta_i^s$ , and the mixing parameter  $\pi_i^s$ .

As with all capture-recapture modeling, the key is to develop probability models describing the events that give rise to the capture history data. Consider the probability associated with the following capture history under sampling situation A:

$$P^A(\text{MUM} | \text{release in period 1 of an animal eventually determined to be male}) \\ = \pi_1 \delta_1^M \phi_1^M p_2^M (1 - \delta_2^M) \phi_2^M p_3^M \delta_3^M.$$

The history MUM denotes an animal caught in period 1, determined to be a male and released. The animal was caught in period 2 and information at that time was inadequate to assign sex. Finally, the animal

was caught again in period 3 and determined again to be male. The initial term in the probability expression is  $\pi_1$ , the probability associated with a new release in period 1 being a male. The next term,  $\delta_1^M$ , denotes the probability that a male caught in period 1 is indeed determined to be a male. The animal then survived until period 2 with probability  $\phi_1^M$  and was caught in period 2 ( $p_2^M$ ). Information available in period 2 did not permit assignment of sex (the probability associated with this event is  $1 - \delta_2^M$ ). The last three parameters in the probability model reflect the probabilities of surviving from period 2 to 3 ( $\phi_2^M$ ), of being caught in 3 ( $p_3^M$ ), and of sex being determined based on information in period 3 ( $\delta_3^M$ ).

Modeling of capture histories for animals determined to be females follows the same sort of logic as used in the above example. Modeling for the third group of animals of unknown sex is slightly more complicated. Consider the probability associated with the following capture history under sampling situation A:

$$P^A(\text{UOU} | \text{release in period 1 of an animal whose sex status is still unknown at the end of the study}) \\ = \pi^1 (1 - \delta_1^M) \phi_1^M (1 - p_2^M) \phi_2^M p_3^M (1 - \delta_3^M) \\ + (1 - \pi^1) (1 - \delta_1^F) \phi_1^F (1 - p_2^F) \phi_2^F p_3^F (1 - \delta_3^F).$$

History UOU indicates an animal caught in periods 1 and 3, but not 2. Sex could not be determined at either capture and thus remains unknown for this animal. The probability model thus includes both the possibility that the animal was a male (probability associated with this event is  $\pi^1$ ) and that it was a female (associated probability  $1 - \pi^1$ ). The subsequent events in the capture history are then modeled as appropriate for males and females, respectively. Finally, the probabilities associated with the two possibilities (that the animal was a male or female) are summed to obtain the probability associated with the capture history. The probability structures for several other capture histories under sampling situation A are provided in Appendix A.

Sampling situation B requires the same parameters and general modeling approach. Capture histories resulting from B contain no Us following the first occasion at which sex is determined. So capture history MUM considered above would be rewritten as MMM under sampling situation B, as every capture following initial assignment as male is automatically written as M. The probability modeling differs from that described above only in that there are no  $\delta_i^s$  following the period at which sex is determined, because subsequent captures provide no information about assignment of sex. For example, the probability associated with capture history MMM under sampling situation 2 would be written as:

$$P^B(\text{MMM} | \text{release in period 1 of an animal eventually determined to be male}) \\ = \pi_1 \delta_1^M \phi_1^M p_2^M \phi_2^M p_3^M.$$

The  $\delta_1^M$  is required for the initial determination of sex,



but no classification parameters are required for subsequent captures. The probability associated with history U0U is identical under sampling situations A and B. Capture histories and associated probabilities under sampling situation B are presented in Appendix B.

The likelihood for the entire capture–recapture study is then written using the above thinking and probability structure. Define  $x_{\omega}^s$  as the number of animals of sex  $s$  (categorized at the end of the study as M, F, U) exhibiting capture history  $\omega$ , and  $u_i^s$  as the number of new animals caught and released in period  $i$  and categorized by the end of the study (period  $K$ ) as sex  $s$ . Further, define  $q_{\omega}^s$  as the conditional cell probability associated with capture history  $\omega$  (e.g., probabilities such as those presented above as examples). The likelihood function for the entire study can then be written generally (e.g., see Williams et al. 2002) as

$$L(\{\phi_i^s\}\{p_i^s\}\{\delta_i^s\}\{\pi_i\}|\{x_{\omega}^s\}\{u_i^s\}) = \prod_{i=1}^{K-1} \frac{u_i^s!}{\prod_{\omega} x_{\omega}^s!} (q_{\omega}^s)^{x_{\omega}^s}. \quad (1)$$

Thus, the numbers of animals in each sex category exhibiting each capture history are modeled as multinomial random variables based on the number of new releases in each sex category at each sampling occasion. The likelihood for the entire study is the product of these multinomials over all cohorts of new releases. Different likelihoods are applicable to the different sampling situations, with the difference determined solely by the differences in the capture histories themselves,  $\omega$ , in the numbers of animals exhibiting each history,  $\{x_{\omega}^s\}$ , and in the probabilities associated with the different histories,  $q_{\omega}^s$ .

The probabilities written for the capture histories in Appendices A and B correspond to general models, in the sense that all parameters are permitted to vary over time (sample periods) and sexes. Reduced-parameter models can be obtained by constraining parameters to be constant over time and/or sex. The models are implemented in LOLASURVIV (written by J. E. Hines, *available online*),<sup>2</sup> which provides maximum likelihood estimates under the general models and various user-defined constraints. The software is based on general program SURVIV (White 1983) and also provides Pearson goodness-of-fit statistics and model selection metrics (AIC, AICc, QAICc; Burnham and Anderson 2002).

#### EXAMPLE ANALYSES

##### Numerical study

We conducted a small numerical study in order to compare five different approaches to the estimation of sex-specific survival and capture probabilities in the face of uncertain sex assignment. We considered a population of 1000 adult males and 1000 adult females.

Males experienced an annual survival probability of 0.80 and females of 0.70. In order to retain a constant population size, 200 new males and 300 new females were added to the adult population each year. Capture probability was 0.50 and the probability of being able to assign sex to a captured animal was 0.30 for both males and females. We generated expected numbers of animals exhibiting each possible capture history (e.g., Nichols et al. 1981, Burnham et al. 1987) and then analyzed these data using five of the approaches described above.

The first approach is termed “naive” and is expected to yield biased results. Histories are divided into three groups, animals eventually classified as males, animals eventually classified as females, and animals whose sex was not ascertained during the study. We have seen this approach used with seabirds, marine mammals, and amphibians, and we believe it is very common. This approach is seldom elaborated in methods sections of capture–recapture analyses, and our knowledge of its wide use comes from questioning analysts about specific analyses. Our prediction is that survival estimates will be biased high for males and females and low for unknowns, because animals that are eventually classified will have been in the marked population longer (i.e., survived longer) on average than animals never classified.

The second approach involves use of multistate models (e.g., Wood et al. 1998), with three states: male, female, and unknown. Under this approach, those animals first classified as unknown sex can transition to one of the two known sex states, after which no transition is possible. This approach is best viewed as an approximation, and some bias is expected because of the heterogeneous survival and capture probabilities among animals of the unknown state (this group is a mixture of males and females). We expect only small bias in most situations, including our numerical example. Because we used parameters constant over time and equal capture probabilities for the two sexes, we fit a standard multistate model (e.g., Brownie et al. 1993) with time-constant sex-specific survival rates and time-constant sex-independent capture probability.

The third approach is ad hoc and involves using only capture history data occurring in and following the sample period in which the animal’s sex is ascertained. So capture history 0UUF0 would be entered into the analysis as 000F0. The two captures (in periods 2 and 3) prior to determination of sex are not used in the estimation. We expect this approach to yield estimates that are unbiased but not as precise as those based on our described models. Because of the manner in which the data were generated, we fit a CJS-type model with time-constant sex-specific survival and time-constant sex-independent capture probability.

The fourth and fifth approaches used likelihoods A and B, respectively, as described above. We expected both models to yield unbiased estimates and predicted

<sup>2</sup> <www.mbr-pwrc.usgs.gov/software>

TABLE 1. Parameter estimates (with standard errors in parentheses) for expected value capture history data generated from a population initialized with 1000 males and 1000 females.

Estimation approach	Survival probability			Capture probability		
	Males	Females	Unknown	Males	Females	Unknown
Naive†	0.86 (0.009)	0.78 (0.012)	0.67 (0.012)	0.54 (0.014)	0.56 (0.016)	0.41 (0.015)
Multistate‡	0.79 (0.012)	0.69 (0.014)	0.76 (0.009)	0.50 (0.009)	0.50 (0.009)	0.50 (0.009)
Ad hoc§	0.80 (0.013)	0.70 (0.015)		0.50 (0.014)	0.50 (0.014)	
Likelihood A	0.80 (0.010)	0.70 (0.011)		0.50 (0.009)	0.50 (0.009)	
Likelihood B	0.80 (0.010)#	0.70 (0.011)#		0.50 (0.009)	0.50 (0.009)	

Notes: The study contained seven sample periods, and 200 new males and 300 new females were added to the population each period. True parameter values were: male survival = 0.80, female survival = 0.70, male and female capture probability = 0.50, and probability of determining sex = 0.30 for both sexes.

† Naive approach grouped histories according to sex categories at the end of the study. Analysis used a three-group CJS model with constant survival and capture probability over time.

‡ Multistate approach used three states: male, female, and unknown, permitting transitions from unknown to either sex. Capture probability is modeled as independent of state.

§ Ad hoc approach used only the portions of capture histories occurring in and following the period of initial determination of sex. A two-group CJS model was used with capture probabilities constrained to be constant across groups.

|| Likelihoods A and B are the two models presented in the text.

# Standard errors are rounded to the nearest 0.001, but are slightly larger for likelihood B than likelihood A.

that model B estimates would be slightly less precise than those obtained under model A. The models assumed time-constant sex-specific survival and time-constant sex-independent capture probability. We also fit a model using likelihood A with all parameters time-specific to check on the identifiability of parameters under this general model.

The results are presented in Table 1 and followed expectations nicely. The naive approach yielded estimates of male and female survival with 7–11% positive bias, and survival of unknown-sex animals with a substantial negative bias. The scenario under which data were generated cannot be viewed as extreme in any way, so that these biases are cause for alarm and provide a clear message that this approach should not be used. The multistate modeling approach yielded a slight negative bias in male and female survival estimates, and the survival estimate for the unknown state was 0.76, reflecting a mixture of the two sexes. The two models presented here and the ad hoc approach using only data in and subsequent to sex determination all yielded unbiased estimates as expected. Precision was best for likelihood A and worst for the ad hoc approach, also as predicted. Precision for estimates under likelihoods A and B was very similar for this scenario, suggesting that more precise estimation of the  $\delta_i^s$  (under likelihood A) contributes little to precision of the survival estimates. Finally, results not presented show that the time-specific model under likelihood A also provided unbiased estimates, indicating no problems with identifiability under this general model.

#### *Roseate Terns at Falkner Island, Connecticut*

In addition to the numerical approximations, we analyzed one of the data sets that motivated our interest in this problem, capture–recapture data on adult Roseate Terns, *Sterna dougalii*, at Falkner Island, Connecticut (see Plate 1). The dynamics of this population

have been well studied both in isolation (Spendelow and Nichols 1989, Spendelow 1991, Spendelow et al. 2002) and in conjunction with other breeding colonies in New York and Massachusetts between Long Island Sound and Buzzards Bay (Spendelow et al. 1995, Lebreton et al. 2003). Although this population has been the subject of several previous capture–recapture analyses, all such analyses have combined sexes, because of the inability to distinguish sex much of the time.

Recent evidence of female–female pairs and sex ratios skewed towards more females at various locations throughout the Long Island Sound/Buzzards Bay (LIS/BB) breeding colonies (Nisbet and Hatch 1999, Nisbet and Spendelow 1999, Szczys et al. 2001) has prompted interest in the sex specificity of survival rates. If there are indeed more females than males among adults, then this sex ratio must arise via a skewed sex ratio at hatching (Szczys et al. 2001) or a difference between male and female survival rates among young or adult birds. In this analysis, we focus on adults sampled at Falkner Island during the period 1993–2002 and assess the hypothesis that survival rates of adult females are greater than those of adult males.

Spendelow's research team records behavioral information relevant to ascertainment of sex whenever possible. Several of these behaviors are regarded as inconclusive (e.g., begging is usually, but not always, done by females) and are not used here. However, two kinds of observation are regarded as definitive: position during copulation and mate feeding when males feed females just before and after egg laying. We thus base our analysis on (mostly color-banded) adult birds captured and resighted multiple times during the breeding season each year as part of one or more behavioral (e.g., Shealer and Spendelow 2002) and population studies. Birds for which observations during the season yielded either no or inconclusive information about sex were recorded as U in the capture history data, whereas

TABLE 2. Parameter estimates for adult Roseate Terns banded at Falkner Island, Connecticut, 1993–2002, under the full model ( $\phi_{t \times s}, p_{t \times s}, \delta_{t \times s}, \pi_t$ ) allowing for uncertainty in classification by sex.

Year ( <i>i</i> )	Survival probability		Capture probability		Classification probability		Probability male for unmarked
	$\hat{\phi}_i^m$ (1 SE)	$\hat{\phi}_i^f$ (1 SE)	$\hat{p}_i^m$ (1 SE)	$\hat{p}_i^f$ (1 SE)	$\hat{\delta}_i^m$ (1 SE)	$\hat{\delta}_i^f$ (1 SE)	$\hat{\pi}_i$ (1 SE)
1993	0.89 (0.072)	0.97 (0.034)			0.51 (0.102)	0.38 (0.092)	0.44 (0.158)
1994	0.85 (0.068)	0.86 (0.055)	1.00	0.97 (0.102)	0.44 (0.093)	0.31 (0.082)	0.56 (0.235)
1995	0.90 (0.124)	0.91 (0.066)	0.94 (0.107)	0.92 (0.108)	0.51 (0.102)	0.44 (0.106)	0.49 (0.232)
1996	0.70 (0.128)	0.86 (0.102)	0.86 (0.297)	0.90 (0.245)	0.39 (0.089)	0.34 (0.106)	0.56 (0.203)
1997	0.77 (0.267)	0.80 (0.138)	0.93 (0.230)	0.88 (0.244)	0.61 (0.136)	0.48 (0.108)	0.39 (0.221)
1998	0.78 (0.171)	0.80 (0.141)	0.97 (0.819)	0.83 (0.305)	0.51 (0.142)	0.43 (0.125)	0.43 (0.198)
1999	0.66 (0.141)	0.70 (0.142)	0.90 (0.351)	0.87 (0.314)	0.58 (0.179)	0.41 (0.138)	0.49 (0.209)
2000	0.71 (0.165)	0.75 (0.187)	0.98 (0.178)	0.84 (0.296)	0.30 (0.160)	0.23 (0.165)	0.60 (0.214)
2001			0.89 (0.235)	0.91 (0.335)	0.40 (0.208)	0.31 (0.176)	0.48 (0.376)
2002					0.45 (0.218)	0.30 (0.135)	0.37 (0.241)

birds conclusively identified as male or female were so recorded. Members of Spendelow's research team record data on sex assignment each year, so the sample situation corresponds to scenario A described above.

We fit a general model with all parameters sex and time specific ( $\phi_{t \times s}, p_{t \times s}, \delta_{t \times s}, \pi_t$ ). This notation uses subscripts  $t \times s$  to indicate a full model with interaction terms between the factors sex and time (sensu Lebreton et al. 1992). In addition, we fit one model with time specificity, but no sex specificity, in survival ( $\phi_t, p_{t \times s}, \delta_{t \times s}, \pi_t$ ), and another model with sex and time as additive effects on survival ( $\phi_{t+s}, p_{t \times s}, \delta_{t \times s}, \pi_t$ ). This latter model hypothesized sex-specific survival rates that varied in parallel over time on the logit scale. Thus one model represented the hypothesis that survival did not vary sex specifically, another more general model included full sex-specificity of all parameters, and an intermediate model hypothesized additive sex and time effects on survival. We also fit other reduced-parameter models but will defer discussion of results to a forthcoming paper focusing on the biological causes and consequences of sex-specific survival.

We evaluated fit of the general model using a parametric bootstrap. Data were generated under the full model ( $\phi_{t \times s}, p_{t \times s}, \delta_{t \times s}, \pi_t$ ) based on the parameter estimates (Table 2). For each generated data set, the deviance-based assessment of fit was computed ( $G^2/\text{df}$ , where  $G^2$  is sometimes termed Wilks' statistic and represents the likelihood ratio test between the saturated model and the model of interest [Agresti 1990]), and a distribution of these values created. The value obtained for the actual data set, 7.26, was very unlikely under the null hypothesis that the model fit the data adequately ( $P < 0.01$ ). Thus, we computed a variance inflation factor,  $\hat{c}$ , by dividing the observed value of  $G^2/\text{df}$  for the data by the mean of the values for the simulated data (White et al. 2001) to obtain  $\hat{c} = 1.21$ . The variance inflation factor was used to adjust model-based variances, where  $\widehat{\text{var}}_{\text{adj}}(\theta) = \hat{c} \cdot \widehat{\text{var}}_{\text{mdl}}(\theta)$ . In addition, we used  $\hat{c}$  to compute QAICc (Burnham and Anderson 2002) for use in model selection.

The model with additive sex and time effects on survival rates had the lowest QAICc value.  $\Delta\text{QAICc} = 2.74$  for the model with survival rates the same for the sexes, providing evidence of sex-specificity in apparent survival.  $\Delta\text{QAICc} = 15.47$  for the most general model, with all parameters time and sex specific. The model selection statistics thus favored the parsimonious modeling of sex and time as additive effects on survival.

Female survival probabilities were higher than those of males under the additive model ( $\phi_{t+s}, p_{t \times s}, \delta_{t \times s}, \pi_t$ ). Under the general model ( $\phi_{t \times s}, p_{t \times s}, \delta_{t \times s}, \pi_t$ ), the point estimates of survival were greater for females than males in every year of the study, with female survival estimates ranging from about 0.70 to 0.95 and male estimates about 0.65 to 0.90 (Table 2). Average survival estimates computed from models (not discussed) in which survival was constrained to be constant over time were about 15–20% larger for females. The results thus support the hypothesis that sex-specific differences in adult survival rate are at least partially responsible for the female-biased sex ratio of this population. Because we are estimating apparent survival, it may be that part of the difference involves permanent emigration. A test of this possibility will require the extension of our modeling approach to multistate models that can use data from the entire LIS/BB metapopulation (e.g., Spendelow et al. 1995, Lebreton et al. 2003).

The estimated probabilities that new, unmarked adults were males ranged from about 0.37 to 0.60. These probabilities tended to be less than 0.5, again favoring females. Estimated capture probabilities were high for both species, ranging from about 0.83 to 1.00 (Table 2). The estimated probabilities of being able to assign sex in a given year ranged from about 0.23 to 0.61.

#### DISCUSSION

Uncertainty is pervasive in the sampling of biological populations. When we survey animals at particular locations, we recognize our counts as representing



PLATE 1. This picture of an unbandied adult Roseate Tern (*Sterna dougallii*) was taken at Falkner Island, Connecticut (USA), in 1979 when research on what would develop later into a comprehensive multisite study was just starting. Recent work on sex-specific differences of adults in feeding their chicks, the female-biased sex-ratio, and the results reported here are providing important new clues about major factors limiting the recovery of the endangered Northeastern U.S. and Canadian breeding population of this species. Photo credit: Patrick J. Lynch.

some unknown fraction of the true number of animals present in the area. Inferences drawn about large areas are based on samples of locations, and there is uncertainty about the animals present in the areas that are not part of this sample. Biologists and statisticians have developed a variety of methods for dealing with these fundamental sources of uncertainty (e.g., Seber 1982, Thompson 1992, Lancia et al. 1994, Thompson et al. 1998, Williams et al. 2002). Here we have focused on an additional source of uncertainty in capture-recapture studies associated with the classification of observed or captured animals with respect to state variables of interest. In a previous paper (Kendall et al. 2003), we provided an approach to dealing with uncertainty in identifying state variables that vary stochastically over time. In this paper, we focus on uncertainty in identification of state variables that do not change over the course of the study. Unlike the situation with stochastic temporal variation in state variables, the situation with state variables that do not change over time can be modeled without the robust design using a straightforward extension of standard models for open populations. However, we still rely on

the assumption that some animals are assigned to state with certainty.

We developed a model for the purposes of deriving reasonable inferences from capture-recapture data in which sex (the state variable of interest) is unknown for some individuals. In addition to the standard survival and capture probability parameters, we included mixture parameters,  $\pi_i$ , for the proportion of males among new animals, and classification parameters,  $\delta_i^s$ , reflecting the probability of being able to assign sex with certainty. For capture histories of animals for which sex was determined at some time during the study, the associated cell probabilities included a single mixture parameter, either  $\pi_i$  or  $1 - \pi_i$ , depending on whether the animal was a male or a female. Cell probabilities for capture histories of animals for which sex was not determined were written as additive mixtures, including the possibilities of the animal having been either male or female (Appendix A, B). The classification parameters were needed for every occasion at which an animal was captured. These parameters reflect a mixture of biological variation (e.g., how frequently do animals exhibit the behaviors that permit unambig-



uous classification) and sampling variation (how much time do investigators spend in the field observing animals).

We first used this model to investigate other approaches that have been used to deal with uncertain sex classification in capture–recapture studies. In particular, we generated expected value data under our general model as a means of approximating the expected value of various estimators. The frequently used (but seldom reported) approach of grouping all animals as known males, known females, and unknown, and then analyzing data with standard capture–recapture models for grouped data produced biased estimates just as predicted. Specifically, the estimators for male and female survival rates are positively biased and those for survival rates of animals in the unknown group are negatively biased with respect to the true survival rate of the mixture. We expect higher survival probabilities and lower capture and classification probabilities to produce larger biases. This analytical approach should be abandoned in favor of the approach presented here.

Other ad hoc approaches included use of external information on sex ratio at banding, use of multistate models with an unknown state, and use of only capture history data following correct classification. These approaches yielded reasonable estimates and performed much better than the naive multigroup approach described above. These ad hoc approaches either required the assumption that true sex ratio of unmarked animals is known (rather than estimated) or yielded small bias (multistate approach) or reduced precision (use of selected capture history data) relative to the modeling approach introduced here. Thus, we recommend the modeling approach presented here as the most appropriate means of dealing with uncertain sex classification but note that the ad hoc alternatives are still much better than the naive multigroup approach.

Finally, we note that this approach can be extended to deal with multiple cues or types of evidence providing information about a captured animal's sex. In this paper, we have considered only evidence that permits unambiguous classification. That is, the evidence is not available for every captured animal, but when the evidence is available, sex is known for that animal with certainty. In some sampling situations, behaviors, morphology, or other evidence may provide cues to an animal's sex that are characterized by uncertainty. For example, Spindelov recorded other behavioral cues that were suspected to be indicative of roseate tern sex, but which were characterized by uncertainty. As long as some cues are known to constitute unambiguous (probability of correct classification = 1) evidence, other cues for which correct classification probability is less than 1 may still provide useful information. Modeling for such cues would include correct classification probability parameters that would be estimated together with the kinds of other model parameters that we have presented.

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#### APPENDIX A

Example capture histories and associated probabilities for a single-age model when an individual's sex may or may not be ascertained at any particular capture/observation occasion (sampling situation A: ascertainment of sex occurs independently at each capture) are presented in ESA's Electronic Data Archive: *Ecological Archives* E085-107-A1.

#### APPENDIX B

Example capture histories and associated probabilities for a single-age model when an individual's sex may or may not be ascertained at any particular capture/observation occasion (sampling situation A: following the period at which sex is assigned, no further effort is made to ascertain sex) are presented in ESA's Electronic Data Archive: *Ecological Archives* E085-107-A2.